SOME PHYSIOLOGICAL ASPECTS OF DROUGHT RESISTANCE IN WINTER WHEAT (*TRITICUM AESTIVUM* L. EM THELL)

By

MAHMOOD OSMANZAI

Bachelor of Science
Kabul University
Kabul, Afghanistan
1969

Master of Science
Oklahoma State Universiy
Stillwater, Oklahoma
1974

Submitted to the Faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the Degree of
DOCTOR OF PHILOSOPHY
December, 1982

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Thesis Approved:

Leroy J. Croy
Thesis Adviser

Harold L. Retzing

Owen G. Merkle

P. Larry Claypool

Norman N. Durham
Dean of the Graduate College

ACKNOWLEDGMENTS

The author wishes to express sincere appreciation to Dr. Lavoy I. Croy, major adviser for his assistance and encouragement throughout the course work and preparation of this thesis. Special appreciation is expressed to Dr. Owen G. Merkle for his assistance in suppling seed and in conducting the field experiment. Grateful acknowledgment is also extended to the other member of my committee, Dr. Darold L. Ketring for his valuable comments. The valuable assistance of Dr. P. Larry Claypool, Professor of Statistics, in the statistical analyses of this study is gratefully acknowledged.

I wish to thank Mr. Gregg Doolittle for his help with planting, laboratory and computer work. I would also like to thank Mrs. Melanie Bayles for the typing of this manuscript.

Sincere appreciation is extended to Dr. Edward L. Smith. I am also grateful to Dr. Mary Beth Kirkham, former Professor of Agronomy. To the Agronomy Department of Oklahoma State University, the auther is grateful for the financial support and the facilities which made this study possible.

I am grateful to my family for their encouragement and understanding during the course of this study.

TABLE OF CONTENTS

LIST OF TABLES

Chapter III

Chapter IV

Chapter V

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Wheat is one of man's principle foods and is grown nearly everywhere in the world. It is the world's major producer of calories and protein. It is also the major cultivated crop in Oklahoma and accounts for over half the total value of crops. As such, wheat is important in programs for increased world food production. The average yield of wheat per unit area is quite low and has not increased significantly in dry areas. Drought stress and lack of irrigation are considered the major limiting factors.

According to Rahja (1966), 36 percent of the world land area is classified as arid to semiarid, receiving only 130 to 760 mm of rainfall annually. Much of the other 64 percent undergoes temporary drought during the crop season. When drought is prolonged, crops fail and many people may starve.

Over the past few years there has been little serious drought in the world, but it is easy to recall the grim years of the early 1970's when severe drought occurred in Asia and Africa. The urgent need for drought studies is recognized by national and international organizations.

Increased yield potential has always been of basic importance in breeding, physiology, management and production programs of many crops.

Understanding of wheat drought resistance mechanisms would help in breeding and developing cultivars with high levels of drought tolerance, and high yield potential under drought conditions.

Research showing how the plant responds to moisture stress has intensified in the last few years, but the main contribution has been to emphasize the complexity of the problem. The physiological understanding of drought resistance is not fully elucidated. The quantitative measurement and relationship of drought resistant plant characters are not fully understood.

The genetics of plant characteristics associated with drought are complex. To breed for a combination of attributes requires the use of (a) a few carefully studied parents; (b) a large population to permit the combination of many favorable genes, and (c) yield testing from early generation (F_3 if practical) onward to homogenity (Hurd 1974).

Drought susceptibility of wheat is a problem in most arid and semi-arid regions of the world, and wherever wheat is grown under less than optimum rainfed conditions.

In view of the multi-faceted nature of drought resistance in terrestrial plants, and the diversity of environmental situations already occupied by crop plants, the task given to the plant breeder of adapting crops to arid environments is an onerous one. Recognition by physiologists and biochemists of various mechanisms which confer some measure of drought resistance should prove useful to plant breeders as they attempt to develop crops for higher yields under drought conditions.

CHAPTER II

LITERATURE REVIEW

Drought Classification

Drought describes the condition in which the available soil moisture is reduced to the point where the plant cannot absorb water rapidly enough to replenish the amount transpired by the plant. Droughts occur as a result of low precipitation, high temperature, and winds, which can reduce yields or cause total crop failure.

Drought itself is not a uniform concept. It is the reaction of the plant to different atmospheric droughts, and soil moisture deficiency, and will also depend on the stage of development at which drought occurs. Kozlowski (1968) classified plants which grow in regions subject to drought into four groups:

1. Drought escape - those plants which mature early and produce seeds before the onset of drought.
2. Drought evasion - those which economize water use and evade drought by conserving the limited moisture supply. This is the most important group, and most cereals grown in semi-arid regions are classified under this group.
3. Drought endurance - those which shed their leaves and endure drought by passing into a dormant condition until water is again available to the roots.

4. Those plants which resist drought by storing up a supply of water to be used when the soil moisture content is below the plant's ability to absorb water.

The ability of the plant to obtain and retain water as well as carry out its metabolism during a period of low tissue water potential is considered drought resistance. Drought resistance is defined by Arnon (1972) as the ability of plants to:

1. survive under drought conditions.
2. endure drought without injury.
3. be efficient in their use of water.

The following definition is reported by Henskel (1964) for drought resistant plants. "Drought-resistant plants are those which in the process of ontogenesis are able to withstand the effect of drought and which can normally grow, develop, and reproduce under drought conditions because of a number of properties acquired in the process of evolution under the influence of environmental conditions and natural selections".

Levitt (1972) divided drought resistance into either drought avoidance or drought tolerance. He stated that the drought avoiding plant maintains a high internal water potential, in spite of low environmental water potential to which it is exposed. Drought tolerance means a plant can survive at low tissue water content or water potential.

Physiological Effects of Drought Stress

Drought stress is used in much of the literature as water stress and water deficit, which expresses the same meaning. Water deficit

occurs in plants whenever transpiration exceeds water absorption.

Water stress is the result of imbalance between the supply furnished by the soil water and the amount needed by the plants. Absorption and efficient use of water through physiological processes of a plant relate to its drought tolerance.

Drought resistance is the result of many frequently independent morphological and physiological characters, whose interaction has not yet been sufficiently elucidated. Most physiological components of resistance are dynamic, and genetical analysis of this hereditary complex has not yet been achieved.

Drought stress does not have a uniform effect upon different aspects of plant growth and development. Some plant processes are relatively insensitive to increasing water stress over the available range, while others are distinctly affected. For example, water stress at flowering reduces yield by reducing the number of kernels per spike and grain weight.

Grain yield, as the final economic product of a crop, is the integrated result of a number of interrelated physiological processes. Stress can affect processes of photosynthesis such as carbon dioxide exchange rate (CER). It can affect growth, which provides photosynthetic tissue, and it can affect reproduction, which provides sinks for the storage of photosynthate. Yield per unit is the result of yield components and the amount of metabolic input. Therefore, photosynthate can be the main factor determining yield.

Photosynthesis

Photosynthetic capacity of plants is determined primarily by total leaf area and the activity of each unit of the leaf. Since CO_2 fixed by photosynthesis represents most of the dry matter accumulated by the plant, any factor that affects photosynthetic activity of the leaves is also likely to affect the total dry matter and, within broad limits, the grain production by the crop. In most cereals, the growth that occurs after flowering is characterized by the photosynthetic products that move to the grain rather than those used for leaf development. During this portion of the life cycle, therefore, changes in the photosynthetic activity of the leaves are an important means by which the photosynthetic capacity of the crop is influenced by drought.

A number of reports have supported the importance of photosynthetic parts and assimilation of carbohydrate in the developing grains of wheat. Some estimates of the contribution to grain dry weight from photosynthesis above the flag leaf node are 60 percent (Archbold, 1942), 85 percent (Asana and Mani, 1950), 83 percent (Enyi, 1962), and 80–85 percent (Quinlan and Sugar, 1965). Langer (1967) found that 83 percent of the grain carbohydrate in wheat was accounted for by the flag leaf and other green parts above the flag leaf node. Thorne (1969) stated that leaf area is of great importance to the grain yield after anthesis. At this period of time, most of the photosynthetic requirement for grain yield is furnished by photosynthesizing parts located above the flag leaf node. Rawson and Hofstra (1969), Hsu and Walton (1971), agreed with Thorne's conclusion that grain yield of cereal plants was closely related to photosynthetic area above the flag leaf.

Lupton and Ali (1966) found that the estimate of varietal differences in photosynthesis of wheat differ by measurement techniques and seasonal variation also occurred. Evans and Rawson (1970) in a study which consisted of 21 lines of both wild progenitors and cultivated wheat found that photosynthetic rate ranged from 27.3 to 45.7 mg $CO_2 dm^2 hr^{-1}$. Gale et al. (1974) in a study of photosynthesis of 8 commercial wheat cultivars found that rates ranged from 12.4 to 19.2 mg $CO_2 dm^2\text{-}hr^{-1}$. The highest rate was found in semidwarf wheat which also produced the highest yield per spike.

The photosynthesis system and its products can be modified by internal and external water stress. Therefore, carbohydrate metabolism can be affected. A number of reports agree on the adverse effect of water stress on photosynthesis of different species of crops. Pallas et al. (1962) stated that as soil moisture-stress increases, photosynthesis decreases. Soil moisture stress and atmospheric drought stress act additively in reducing the rate of photosynthesis (Baker and Musgrave 1964). Ashton (1956) stated that leaf area is more affected by water stress than for net assimilation rate.

Slatyer (1967) stated that, in general, net photosynthesis is progressively reduced by water stress, and under severe stress negative values may develop i.e., respiration can become greater than photosynthesis. It is assumed that this response is mediated partly by the amount of impeded CO_2 supply following stomatal closure and partly by a direct effect of dehydration on the photosynthetic system. In a study with cotton leaves Troughton (1969) observed that reduction of net photosynthesis occurred as the severity of stress was increased.

Stomatal Behavior

Many studies have been done to assess the relative importance of stomatal closure and dehydration.

Stomata have a significant role in controlling water loss by transpiration of and diffusion of CO_2 into the plants. Therefore, stomatal behavior (opening or closing) can be used as an indicator of whether transpiration and photosynthesis may be occurring.

The need for understanding stomatal physiology and quantification of the diffusive resistance of stomata to water vapor and CO_2 has been recognized by many researchers. "The status of stomata in a plant or leaf is dynamic and they change in response to many environmental and endogenous factors. In addition, stomatal behavior can vary from species to species, in some instances, dramatically" (Kanemasu, 1975).

Stomatal Opening and Water Stress

There are many factors which affect stomatal opening and closure, such as water stress, light intensity, temperature, CO_2, humidity, leaf age, nutrition and disease, and endogenous rhythms (Hsiao, 1973).

Water stress and light intensity are two predominant factors affecting stomatal opening under field conditions. It is a well-known phenomenon that leaf water potential induces partial to complete stomatal closure. However, the relationship between stomatal opening and leaf water status is not linear and can be complex. Kanemasu (1975) proposed use of stomatal opening as indicator of water stress. Estimates of plant-water deficit can be obtained, using stomatal resistance, which is a more sensitive measure than relative water

content (Al-Ani and Bierhuzen, 1971). Stomatal opening is caused by turgor changes and fluctuation between guard cells and their adjacent cells (Waggoner and Zelitch, 1965).

Considerable quantitative data on stomatal resistance and plant water status are reviewed by Hsiao (1973) and indicate that in many species stomata are unaffected by leaf-water status until the water potential or content is decreased beyond a threshold level. The level varies with species and may vary with growing conditions. In many cases, the range is -8 to -12 bars of leaf water potential. Reduction beyond the threshold level causes stomatal closure even at 2 to 3 bars. Thus stomatal opening is related to severity of stress. Stout and Simpson (1978) reported that stomata in sorghum close later than stomata in corn. This might be related to the drought resistance of sorghum.

Stomatal Opening and Photosynthesis

Stomatal opening and closing have a direct effect on the amount of CO_2 which is fixed by the leaf. Brown and Rosenberg (1970) reported that due to closure of stomata under water stress, diffusive resistance to CO_2 exchange increases, apparently photosynthesis decreases as a result of this, and reduction in yield occurs. Troughton (1969) and El-Sharkawy and Hesketh (1964) reported a correlation of photosynthetic reduction during stress with stomatal closure. If stomatal resistance is the major resistance in the pathway of CO_2 diffusion, photosynthesis will be affected by stomatal action. Therefore, a quantitative study of photosynthesis, understanding of stomatal diffusive resistance is important.

Implications of Different Drought Resistance Mechanisms

Drought resistance mechanisms of interest to the agronomist are most often couched with a concern for productivity, whereas those of interest to the ecologist are most often concerned with survival. The metabolic basis of productivity on the one hand and survival on the other are likely to be very different and are often difficult to compare. Much attention has been given recently to productivity and survival in water limited environments. Little attention has been given to photosynthetic processes in illuminated leaves deprived of external CO_2 due to stomatal closure, the most common of all responses to water stress, and the basis of drought resistance mechanisms related to control of water loss. Midday stomatal closure in crops (Turner and Begg, 1978) limits carbon assimilation, but may optimize carbon assimilation in relation to water use on a daily basis.

Survival of plants during periods of extreme desiccation may be based on functional metabolic systems which are isolated from the environment, as in the case of rhizomes on the leaf and stem of succulents. In the literature dealing with structural and biochemical changes which accompany dehydration and rehydration of desiccation tolerant plants, parents are almost always sought with changes which follow desiccation of conventional mesophytic plants.

More stable changes in metabolic systems could be involved in drought resistant plants exposed to much lower levels of stress. The various forms of solute accumulation may reflect either the redirection of metabolic products or major changes in metabolic patterns. For

example, sugar may be retained in cells of expanded leaves and accumulated in the vacuole in order to maintain leaf turgor or may be translocated to the root to maintain growth of new roots which may be functional in water uptake rather than being translocated and used in development of new leaves and production of additional light trapping surface.

It would appear reasonable to presume that a cultivar with high nitrate reductase activity shortly after survival from water stress would have an advantage, as it would be able to reduce nitrate more rapidly to support renewed protein synthesis. It is highly likely that the conservation of energy is an essential requirement for survival during stress, so that a rapid loss of nitrate reductase activity would be a metabolic advantage. In fact, definitive experiments have yet to be performed to determine the magnitude of nitrate assimilation during water stress (Sinha and Nicholas, 1981).

The phenomenon of proline accumulation by plant tissues during water deficit has attracted considerable attention since it was first described, but the precise role of proline in the metabolism of the stressed plant remains to be elucidated. There is considerable evidence, however, from a range of sources which supports the proposition that proline accumulation is positively correlated with drought resistance.

Further progress in understanding proline accumulation and its possible utilization in programs with practical objectives awaits clarification of its role in the metabolism of the plant during water deficit. This objective will be aided by the development of plant strains which differ markedly in proline accumulation but in little

else. The selection of such strains may also provide information on the genetics of the response which will be of use in future breeding programs. It is undoubtedly premature at this juncture to breed varieties with a high proline accumulation potential for use in practical agriculture, if only because the techniques needed have not as yet been formulated. It is reasonable to expect, however, that proline accumulation, together with other objective physiological criteria of plant resistance to water deficit, will complement field testing in future cereal breeding programs.

Quarrie and Jones (1977) studied the effect of ABA and water stress on development and morphology of wheat in two different experiments. In both experiments the treated plants produced smaller leaves and fewer spikelets per spike. Analysis of epidermal morphology showed that both ABA and water stress decreased the mean cell size, reduced the number of stomata per leaf, and increased the production of trichomes in all the leaves sampled. Data for stomata length and stomatal indices showed that differences between a main stem leaf and a tiller leaf were consistent for both experiments. It was concluded that ABA could mediate many of the responses of wheat plants to prolong water stress.

A correlation between ABA increase and proline accumulation under stress conditions is evident. Experimental application of ABA increases the concentration of free proline in leaves. This fact suggests that amino acid metabolism under stress is mediated by hormonal balance with the prominent importance of ABA (Singh et al., 1972).

Genotype variation in ABA and proline accumulation during water stress recently has been more extensively studied. The incorporation of

the ability for high ABA and proline accumulation in crops under water stress in breeding programs requires intensive field assessment for improving crop drought resistance.

The influence of the root system on drought resistance of a plant has been discussed primarily in terms of its ability to maximize the amount of water it collects while also insuring also that the way in which the water is collected through time is appropriate to the plant environment. These primary aspects have been discussed against a background of more detailed phenomena that have no obviously direct bearing on drought resistance, such as the factors affecting the rate of transport of water from soil to shoot, and the factors affecting the rate and extent of root growth.

Water use efficiency (WUE) is another aspect of plant productivity in dry conditions. It is, considered here initially as the net CO_2 uptake per unit of transpiration ($mgCO_2\ gH_2O^{-1}$), and can be determined with gas exchange measurement of illuminated photosynthetic tissue.

Agronomists often report that improved management (e.g. fertilization, planting density, etc.) and plant breeding have led to substantial gains in WUE terms of yield of economic product per unit of water supplied. However, it is unlikely that WUE as it has been defined (total dry matter per unit transpiration) has increased. Most of the gain reported derives from an increase in transpiration as a fraction of water supply due to greater soil extraction and greater plant reducing soil-evaporation, or from an increase in harvest index.

A multitude of change in the morphology of leaves and other green organs appear to be correlated with adaptation to increasing aridity and xerophytism. Specific leaf density (leaf weight per unit area)

generally increase with aridity. Leaf density not only favors survival but also photosynthetic ability at very low leaf water potential. However, it is also associated with low maximal rates of photosynthesis. Specific leaf density varies between crop species and cultivars and tend to be positively associated with photosynthetic rate per unit leaf area. Within the Triticum genus it has been suggested that the better adaptation to drier environments of their more primitive members compared to the more mesophytic cultivated species is associated with smaller, denser, leaves having a greater ratio of vascular tissue to photosynthetic tissue and a greater photosynthetic rate.

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CHAPTER III

A NONDESTRUCTIVE MEASUREMENT OF LEAF AND LEAF SEGMENT AREA IN WINTER WHEAT (TRITICUM AESTIUUM L. EM THELL)

Introduction

Leaf area measurements are often needed as an index for photosynthate assimilation and transpiration in crop physiological studies. Photosynthesis is usually measured as carbon dioxide exchange rate (CER) per unit area of leaf per unit of time.

The numerous methods devised for measuring leaf area is reviewed by Marshall (1968). Hatfield et al. (1976) discussed and evaluated the use of an electronic area meter for measuring leaf area. This method improved accuracy and rate of measurement over the older light interception photoelectric planimeters (Gunther, 1948; Marshall, 1968).

Several investigators have studied the association between leaf area and leaf fresh or dry weight. A high correlation was obtained (Watson, 1937). Aase (1978) reported a high correlation between leaf area and leaf dry matter (r=0.951).

Measurement of CER using infrared analysis and a plexiglass chamber was introduced by Sullivan et al. (1976) and modified by Huber (1978) and Bruns (1981). These methods require the leaf segment area for reporting the CER per unit area of the leaf.

One of the most frequently used nondestructive and indirect, but

accurate, methods is that of estimating leaf areas from mathematical formulas involving linear measurement of the leaf. The usual procedure involves measuring length (L), width (W) and area (A) of a sample of leaves and then calculating one of several possible correlation coefficients, regression equations, or leaf factors, K=LW/A or K=A/LW, for estimating areas of subsequent samples (Wiersma and Bailey, 1975; Osmanzai, 1974). The advantages and accuracy of this method are discussed by Marshall (1968) in his review and by Kemp (1960).

Several mathematical formulas have been derived from estimating leaf areas of numerous crops, but there is little information available for flag leaf, a segment or portion of flag leaf. Several investigators have shown the importance of photosynthesis of the flag leaf to grain yield of wheat. Voldening and Simpson (1967) reported that the spike and flag leaf contributed a major portion of photosynthate to the grain weight. Thorne (1966) stated that the flag leaf has a great influence on grain yield after the plant heads.

In this paper determination of flag leaf area and flag leaf segment area by measuring L and W is presented.

Materials and Methods

Flag leaf samples were obtained from the Wheat Architecture Nursery at the Agronomy Research Station in Stillwater, Oklahoma during the 1980 growing season. The nursery consisted of 30 cultivars grown in a randomized block design with three replications planted on October 17, 1979. Each plot had 4 rows that were 3 m long with 30 cm between rows. The seeding rate was 1000 kernels per plot.

A sample of 20 flag leaves was randomly taken from each plot over

the three replications of 7 cultivars (Table I). The flag leaf length, width and area of each leaf in the sample were measured in the laboratory. The flag leaf length (L) was measured from the tip of the leaf to the ligule to the nearest 0.01 cm. The leaf width (W) was measured at the maximum width of the leaf.

Leaf area (A) was measured by passing the leaf through the leaf area meter model LI-COR LI3000, and the area of a leaf segment (SA) by cutting of a leaf segment at maximum leaf width. The length used (6.4) inside the chamber. The general linear model was used for formulating the equation for estimation of leaf and segment area. The corrected R^2 was calculated as described by Draper and Smith (1982).

Results and Discussion

The cultivars have comparable heading dates, while their heights range from 84-104 cm of height. Number of tiller per 30 cm^2 varied from 38 to 55. Means of flag leaf area, length, width and segment area are reported in (Table II).

Regression Analyses

An important consideration in formulating prediction equations by regression analysis is the choice of the independent variable(s). Three prediction equations were used to estimate flag leaf area as follows:

$$(1)\quad Y_i = \beta_0 + \beta_1(LxW) + \beta_2 W$$

$$(2)\quad Y_i = \beta_0 + \beta_1(LxW) + \beta_2 L + \beta_3 W$$

$$(3)\quad Y_i = \beta_1(LxW) + \beta_2 L + \beta_3 L^2$$

TABLE I

NAME AND ORIGIN OF SEVEN WINTER WHEAT CULTIVARS

No.	Cultivars		Origin
1.	Bezostaia I	(Be)	USSR
2.	Priboy	(Pr)	USSR
3.	Sturdy	(St)	USA-Texas
4.	Partizanka	(Pa)	Yugoslavia
5.	Blueboy	(Bl)	USA-North Carolina
6.	GK Protein	(GK)	Hungary
7.	NR 391-76	(NR)	Austria

TABLE II

MEANS FOR FLAG LEAF LENGTH, WIDTH, AREA AND SEGMENT AREA OF SEVEN WINTER WHEAT CULTIVARS

Cultivar	Length, cm	Width, cm	Area, cm^2	Segment Area, cm^2
Be	19.02	1.55	21.45	8.84
Bl	18.30	1.71	21.96	9.44
GK	19.80	1.59	22.72	8.99
NR	19.84	1.61	24.50	9.17
Pa	19.90	1.45	20.92	8.24
Pr	18.67	1.52	21.46	8.68
St	17.28	1.42	16.31	7.93

Equation (3) was modified by retaining only the terms have significant regression coefficients. Thus for two cultivars Be and St only the (LxW) term remained in the equation while (LxW) and L remained for three other cultivars (Bl, GK, and Pa), and the complete equation (3) was applied to the remaining two cultivars (NR and Pr). Also, two prediction questions were used to estimate leaf segment area:

$$(4) \quad Y_i = \beta_0 + \beta_1(LxW) + \beta_2(LxW)^2$$

$$(5) \quad Y_i = \beta_1(LxW)$$

Results of the analyses of these models are presented in Tables III to VI.

For the three models used to estimate flag leaf area of specified cultivars the R^2 values provide no basis for using one model over the others. Even though use of equations (1) and (2) provided virtually no significant regression coefficients when tested individually. These prediction equations were just as effective for estimating flag leaf area as equation (3) which gave significant coefficients (compare Tables III, IV and V). Thus choosing equation (1) or (2) as opposed to equation (3), modified to retain only those terms have significant coefficients, is simply a matter of preference. Choice of equation (1) provides a prediction equation which contains the same components for all cultivars; while choice of equation (3), as modified, provides the simplest equation possible to use. Also equation (3) (see Table V) provides a grouping of cultivars according to leaf shape.

The coefficients of regression for flag leaf segment area are reported in (Table VI). Segment area was estimated by use of (LxW) and $(LxW)^2$. Since the L was common for all samples, then only (W) was measured. On the basis of the result, (LxW) was chosen the independent

TABLE III

COEFFICIENTS OF REGRESSION FOR FLAG LEAF AREA OF SEVEN WINTER WHEAT CULTIVARS

Cultivars	Parameters			R^2	CV
	Intercept	LxW	W		
Be	2.73	0.71	-1.61	0.82	8.46
B1	4.24	0.73	-3.12	0.95	6.09
GK	10.87	0.97	-11.21	0.83	8.78
NR	7.19	0.85	-6.32	0.96	4.29
Pa	5.67	0.74	-4.23	0.89	6.16
Pr	6.92	0.88	-7.07	0.94	5.66
St	2.50	0.56	-0.01	0.75	8.54

TABLE IV

COEFFICIENTS OF REGRESSION FOR FLAG LEAF AREA OF SEVEN WINTER WHEAT CULTIVARS

Cultivars	Parameters				R^2	CV
	Intercept	LxW	L	W		
Be	1.89	0.69	0.04	-1.06	0.83	8.51
B1	-9.63	0.27	0.81*	4.74	0.95	5.93
GK	-9.52	0.27	1.03	1.99	0.83	8.79
NR	-4.13	0.47	0.62	0.63	0.96	4.29
Pa	-23.18	-0.26	1.46	15.47	0.91	6.02
Pr	0.69	0.67	0.32	-2.99	0.94	5.70
St	-0.14	0.44	0.17	1.78	0.75	8.58

*PR > |T| for testing of H_o parameter is equal to zero. $\alpha = 0.05$.

TABLE V

COEFFICIENTS OF REGRESSION FOR FLAG LEAF AREA OF SEVEN WINTER WHEAT CULTIVARS

Cultivars	Parameters			R^2	CV
	LxW	L	L^2		
Be	0.72**	-	-	0.83	8.36
St	0.66**	_	-	0.73	8.75
B1	0.57**	0.21*	-	0.95	6.00
GK	0.51**	0.32*	-	0.81	9.08
Pa	0.53*	0.28**	-	0.90	6.04
NR	0.50**	0.25*	0.01**	0.96	4.23
Pr	0.50**	0.13*	0.01**	0.94	5.36

*Significant at 0.05.

**Significant at 0.01.

TABLE VI

COEFFICIENTS OF REGRESSION FOR FLAG LEAF SEGMENT AREA OF SEVEN WINTER WHEAT CULTIVARS

	Parameters				
Cultivars	Intercept	LxW	$(LxW)^2$	R^2	CV
Be	-3.85	2.04	-0.07	0.68	5.00
B1	7.34*	-0.60	0.08*	0.87	4.41
GK	19.28**	-3.31**	0.21**	0.80	3.92
NR	0.49	0.94	-0.00	0.82	3.07
Pa	0.82	0.99	-0.01	0.82	3.77
Pr	-3.23	2.03	-0.08	0.48	7.65
St	0.00	1.06	-0.01	0.85	3.42
After dropping the intercept and $(LxW)^2$ from the equation the (LxW) becomes significant.					
Be		0.98**±0.006		0.65	5.19
B1		0.95**±0.006		0.86	4.58
GK		0.97**±0.006		0.64	5.19
NR		0.98**±0.003		0.81	3.05
Pa		0.98**±0.005		0.77	4.27
Pr		0.98**±0.01		0.36	8.36
St		0.96**±0.004		0.84	3.47

*Significant at 0.05.

**Significant at 0.01.

variable for subsequent regression analyses. Using LxW as the only independent variable the R^2 increased to 0.99. However the corrected R^2 was calculated and used (Draper and Smith, 1980). Using the LxW as the only variable resulted in a small decrease in R^2, but this is negligible.

The results indicate that a considerable saving of time, without loss of predictability could be possible by measuring of only leaf width and using K for estimation of segment area. Based on the analyses and testing for zero intercept a factor (0.97) as a constant (K) in the equation of SA = (0.97x6.4)W was found.

Summary

The relationship between leaf area and LxW was linear. In prediction of leaf area by use of a regression equation, cultivars with similar leaf shape could be possibly grouped. LxW was found as an important variable in prediction of leaf area.

A factor K=0.97 was found to be significant in determination of leaf segment area by only measuring leaf width in the equation of S A = K(LxW). This indicates that a considerable savings of time, with little loss of predictability, could be possible by only measuring leaf width to estimate leaf area of a given segment length.

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CHAPTER IV

CARBON DIOXIDE EXCHANGE RATE, STOMATAL DIFFUSIVE RESISTANCE IN RELATION TO DROUGHT RESISTANCE IN WINTER WHEAT (TRITICUM AESTIVUM L. EM THELL)

Introduction

Plants transpire much more water than is used for growth and metabolism. Efficiency of water use is a major social and economic issue. One physiological character which is under metabolic control is stomatal aperature which reduces plant water loss by transpiration.

Regulation of gas exchange between the plant and atmosphere is an important physiological trait in relation to water use. Both H_2O vapor and CO_2 movement between the atmosphere and leaf is mostly restricted to effusion through stomata in the leaf surface. The rate of diffusion of a gas through a pore is a function of pore size, boundary layer effects, the molecular weight of the gas, the concentration gradient of the gas and some other parameters. Each of these contributes a resistance factor to gas flow.

Stomata are the control points in the sequence of resistance because by opening or closing, their resistance can change by a factor of about 10. The degree of opening is determined by guard cell turgor pressure. The more turgid the guard cells are the wider the opening.

It is now well established that this turgor pressure is maintained by potassium ion uptake from the surrounding epidermis, Zelitch (1969), Hsaio et al. (1973). Metabolic energy to operate this potassium pump is derived from photosynthesis, and is closely related to glycolate metabolism (Zelitch, 1969). From the atmosphere to the mesophyll cell wall the pathway of both CO_2 and water is the same. Although the resistance of CO_2 is 1.7 times that of water due to its larger and heavier molecule, CO_2 also encounters a vastly greater mesophyll resistance than does water. Hence the stomatal resistance represents a smaller portion of total resistance to CO_2 than water vapor diffusion. That means a partial closure of the stomata should reduce transpiration more than it reduces photosynthesis. Zelitch (1971) stated that although dry matter production is reduced, the transpiration ratio or water use efficiency is improved. Water loss is relative, however, and some plant species or cultivars are much more efficient than others in terms of water consumed per unit of dry matter produced.

I proposed to determine whether some cultivars have a higher CER in relation to stress level. If this is true and this relationship is under genetic control, then hopefully plant productivity can be increased by increased water use efficiency.

Materials and Methods

The study was conducted under controlled conditions to induce artificial drought stress from heading to maturity in the Controlled Environment Laboratory (CERL) at Oklahoma State University.

Five winter wheat cultivars having diverse genetic backgrounds were planted in plastic pots holding 600 g of Kirkland silt loam mixed with

peatmoss at 2 to 1 v/v ratio. Five seeds were planted/pot and after emergence seedlings were thinned to three plants/pot. One week after planting seedlings were exposed to cold treatments with temperature 7/1 C day/night with an 8-hour light period for vernalization in a chest type growth chamber. After 46 days of vernalization the plants were transplanted to plastic pots (17 cm deep X 15 cm diameter) holding 2.4 kg of soil. Growing media was a mixture of 1 part peat moss and 3 part soil. Fertilizer was added to the soil mixture at the rate of 5 $g10^{-3}m^{3}$ 18-46-0 ($N-P_2O_5-K_2O$). After transplanting pots were transferred to a growth chamber with a 14 hour photoperiod and irradiation flux density 550 $\mu Em^{-2}sec^{-1}$ at plant level and temperature of 21/14 C day/night.

The experiment was designed as a split plot in a randomized block design with wheat cultivars as the main plot treatment factor and water stress levels as the subplot treatment factor.

All pots received the same amount of water to heading stage. Water levels were normal or non-stressed, moderate stress (2/3 normal), and severe stress (1/3 normal). The normal non-stress treatment received was watered based on water holding capacity of the soil in the pot.

Measurements were taken 6 hours after the lights were turned on, prior to rewatering. Measurements were taken on the last fully exerted flag leaf beginning at the heading stage.

A single measurement of photosynthesis (Ps) and stomatal diffussive (Rs) was made from each pot at each sampling period.

Photosynthesis measurements were taken on a single flag leaf placed in a plexiglass chamber 6.4 cm long X 2.9 cm diameter. A Beckman Model 865 infrared gas analyzer was used to determine carbon dioxide exchange

rate (CER) as a measure of photosynthesis. A Beckman Model 1005, 10 inch chart recorder was used to record data. The syringe method developed by Sullivan et al. (1976) Clegg et al. (1978) and modified by Huber (1978) and Bruns (1981), was used.

A gas sample of 6 to 7 cm^3 was withdrawn using a 10 cm^3 hypodermic syringe while the leaf was in the dark then it was illuminated for 60 seconds after which a second sample was taken. Syringes containing gas samples were brought to the laboratory. The samples were adjusted to 5 cm^3 and then injected into the infrared gas analyzer via a stream of lamp grad nitrogen (flow rate of 1 liter min^{-1}) to determine CO_2 concentration. Photosynthesis was determined by the rate of CO_2 exchange per unit leaf area. Since the measurements were taken on each pot during grain filling, a non-destructive procedure (Osmanzai, 1982) was used to determine the leaf segment area that was used for photosynthesis.

$$\text{Leaf SA} = (L \times W) \times K$$

where L = length of the leaf chamber

W = width of flag leaf

K = correction factor (0.97) to correct for the flag leaf segment shape.

Stomatal diffusive resistance Rs was measured by using a Model LI-65 autoporometer and diffusive resistance sensor LI-205, Lambda Equipment Corporation, Lincoln, Nebraska. The equipment was calibrated according to methods of Kanemasu et al. (1969). The measurements were taken from the upper surface of the same flag leaf used for photosynthetic measurements. Leaf area of five fully exerted flag leaves were measured using a portable LI-COR LI3000 leaf area

meter. Tiller count was based on the number of tiller bearing heads of 3 plants per pot.

Kernels per spike were determined based on total number of kernels divided by the number of productive tillers. Kernel weight was determined by dividing the grain yield by the number of kernels.

Plant height was measured from the soil surface to the tip of the terminal spikelet (excluding awns).

The total dry matter of each pot (three plants) was measured after oven drying.

Grain yield was based on the weight of threshed and cleaned grain of each pot and was expressed in grams per pot.

Data were analyzed by pooling the measurements of each variable over time for genotypes and stress levels. Simple as well as multiple correlation and regression were carried out on the data to indicate the association of characters with stress levels of the genotypes.

Results and Discussion

Water use efficiency (WUE) has important implications in areas where water supply is limited and crops are often subjected to soil moisture stress. The influence of soil moisture stress on plant growth and crop production is of great importance.

The agronomic performance of five winter wheat cultivars grown under three water levels is reported in Tables I and II. There is a significant difference in total dry matter production of the cultivars averaged over replications and water levels. The tall types accumulated the highest total dry matter and the semi-dwarfs the lowest. There was no significant difference between the cultivars for grain production and

TABLE I

SOME AGRONOMIC CHARACTERS OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Cultivars	Total Dry Weight g	Grain Yield g/pot	Harvest Index	Height cm
Blue Jacket	31.0* a**	7.9 a	0.25 b	70 a
Kan King	27.1 b	7.6 a	0.27 ab	69 a
TAM-101	25.3 bc	8.2 a	0.32 ab	58 b
Vona	24.5 c	8.2 a	0.34 a	57 b
Sturdy	24.0 c	6.2 a	0.25 b	55 b
P > F	0.0002	0.27	0.09	0.01
* mean of N(9)				
Stress Levels				
Non-stress	29.9* a**	8.6 a	0.28 a	64 a
Moderate stress	26.6 b	7.6 b	0.28 a	63 a
Severe stress	22.64 c	6.7 c	0.30 a	59 a
P > F	0.0001	0.0001	0.35	0.48
CV %	5	12	11	19
*mean of N(15)				
**α = 0.05				

TABLE II

YIELD COMPONENTS OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Cultivars	Productive Tiller No.	Kernel/Spike	Kernel Weight mg
Blue Jacket	14* b**	18 a	32.2 b
Kan King	14 b	23 a	35.3 a
TAM-101	16 a	20 a	27.4 c
Vona	15 a	23 a	23.9 d
Sturdy	17 a	16 a	23.3 d
P > F	0.04	0.31	0.0001
*Mean of N(9)			
Stress Level			
Non-stress	18* a**	18 a	27.5 b
Moderate stress	15 b	22 a	28.3 a
Severe stress	12 c	19 a	29.5 a
P > F	0.0001	0.36	0.049
CV %	18	45	7
*Mean of N(15)			
**α = 0.05			

kernels/spike. However, there was a significant difference in harvest index (HI), plant height, number of tillers and kernel weight.

In response to water-stress across replications and cultivars, total dry matter grain production and tillers decreased significantly as water-stress increased. The lowest number of tillers resulted in heavier kernel weight under water stress. The results suggest that the reduction of grain production under water stress is due to a reduced number of productive tillers.

In general terms, WUE is increased by optimizing all of the factors that promote growth. Photosynthetic CO_2 fixation is the source of most plant dry matter; therefore the rate of this process may limit crop yields. Changes in the net rate of CO_2 assimilation reflects changes in both stomatal conductance and mesophyll capacity for photosynthesis. One way to increase WUE through modification of CO_2 metabolism is to suppress photorespiration (Marx, 1973). One approach is to inhibit photorespiration by inactivation of an enzyme such as glycolic oxidase through mutation (Tinus, 1974).

There also is evidence that the photosynthetic rate, total dry matter, and even seed yield are highly correlated in wheat (Lupton, 1969). Increasing the CER is considered another approach to increase WUE in winter wheat.

CER and Rs of five winter wheat cultivars under three moisture levels are reported in Table III. There was no significant difference in Rs between cultivars. CER was significantly different among cultivars. Blue Jacket had the highest CER followed by Kan King and TAM-101.

TABLE III

SOME PHYSIOLOGIC CHARACTERS OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Cultivars	Stomatal Resistance (Rs) sec cm^{-1}	Carbon Dioxide Exchange rate mg dm^{-2} hr^{-1}	Leaf Area cm^2
Blue Jacket	69.9* a**	4.55 a	10.9 ab
Kan King	65.6 a	3.70 ab	8.7 b
TAM-101	52.9 a	3.44 ab	12.1 a
Vona	54.5 a	2.92 b	11.2 ab
Sturdy	47.4 a	2.97 b	9.1 b
P > F	0.37	0.05	0.08
*Mean of N(9)			
Stress Level			
Non-stress	50.0* b**	3.9 a	12.2 a
Moderate stress	50.8 b	3.6 ab	10.4 a
Severe stress	71.6 a	3.1 b	10.6 a
P > F	0.0002	0.06	0.79
CV %	22	25	12
*Mean of N(15)			
**α = 0.05			

Under severe water stress the Rs values increased significantly, while CER decreased significantly. The results suggest that the reductions of grain yield and total dry matter production under drought condition may be due to inhibition of photosynthesis. This does not necessarily mean that the increase of stomatal resistance caused the reduction of photosynthesis because the same cultivars had both high CER as well as higher Rs.

Total dry matter production and grain yield of five winter wheat cultivars under three levels of water-stress averaged over replications are presented in Table IV and Fig. 1. There was a reduction of 17 to 30% in total dry matter production between non-stress and severe stress and varied with genotypes. Total dry matter production of Sturdy was only reduced 17% under severe-stress because it was an early maturing cultivar and the period of water-stress was shortened. Grain yield was reduced at the same manner. Grain yield of all cultivars was reduced as a result of reduction in productive tiller number. In other words, severe water-stress reduced the productive tiller number from 17 to 45% of non-stress treatment. Kernels per spike were reduced 11% for Sturdy (Table V). A 45% reduction in productive tiller number of TAM-101 resulted in an increase in kernels per spike and kernel weight due to negative relationships among yield components.

Rs and CER for each cultivar are presented in Table VI and Fig. 2 and 3. Rs increased 28 to 53% under the severe-stress. Rs of Blue Jacket increased 46% under the severe-stress. This resulted in 13% reduction of CER, while Rs of Sturdy increased 53% under severe-stress accompanied by 44% reduction of CER. This mechanism could provide

TABLE IV

RELATIVE CHANGES IN FIVE WINTER WHEAT CULTIVAR FOR DRY MATTER AND GRAIN YIELD UNDER THREE MOISTURE LEVELS

Characters	Cultivars				
Stress levels	Blue Jacket	Kanking	TAM 101	Vona	Sturdy
Total Dry Matter					
NS	35.3 a*	29.8 a	29.0 a	28.7 a	26.4 a
MS	31.3 b	28.6 a	24.8 b	24.7 b	23.6 b
SS	26.4 c	22.9 a	22.0 c	20.0 c	21.9 b
% Reduction	25	23	24	30	17
Grain Yield					
NS	9.4 a	8.5 a	9.1 a	9.1 a	6.6 a
MS	7.8 b	7.8 a	7.5 b	8.6 a	5.9 a
SS	6.5 b	6.4 a	7.9 ab	7.0 b	6.0 a
% Reduction	31	25	14	24	10

NS - Non stress

MS - Moderate stress

SS - Severe stress

*Significant at 0.05.

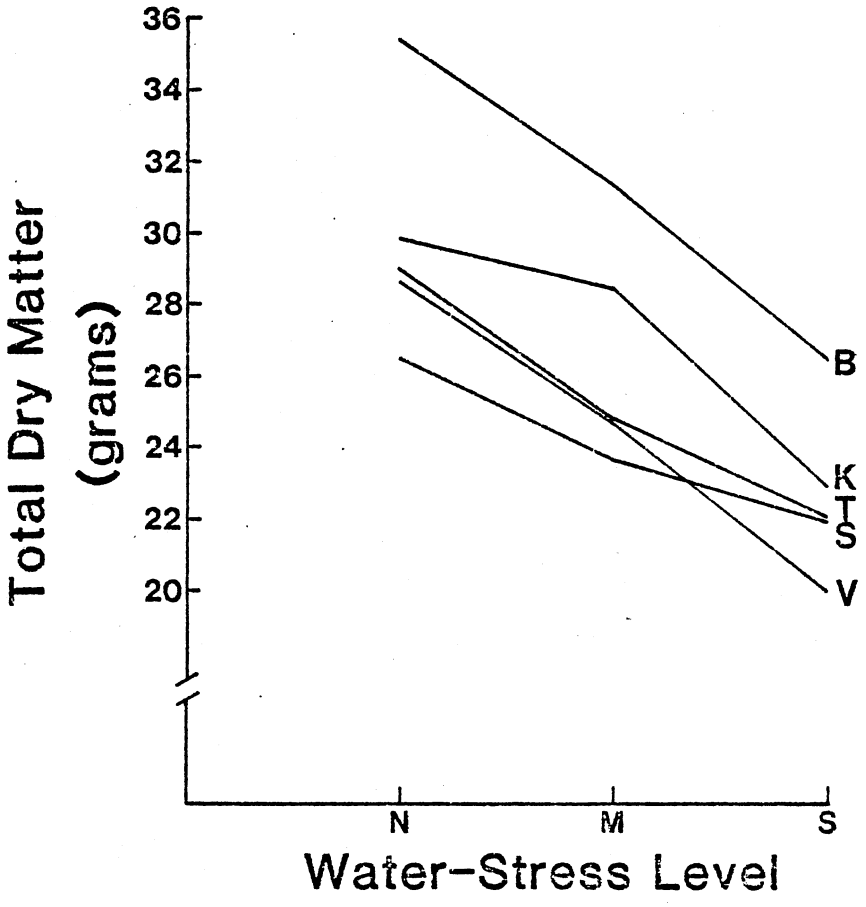

Figure 1. Total Dry Matter of 5 Winter Wheat Cultivars Under 3 Levels of Water-Stress

TABLE V

RELATIVE CHANGES IN FIVE WINTER WHEAT CULTIVARS FOR YIELD COMPONENTS UNDER THREE MOISTURE LEVELS

Characters	Cultivars				
Stress levels	Blue Jacket	Kanking	TAM 101	Vona	Sturdy
Productive Tiller No.					
NS	16 a*	18 a	22 a	16 a	18 a
MS	15 ab	13 b	13 b	16 a	18 a
SS	11 b	11 b	12 b	12 a	18 a
% Reduction	31	39	45	25	17
Kernels/spike					
NS	18 a	16 b	16 a	21 a	17 a
MS	18 a	37 a	20 a	22 a	16 a
SS	18 a	16 b	22 a	26 a	15 a
% Reduction	0	0	-	-	11
Kernel weight/mg					
NS	32.2	33.1	25.9	25.3	21.0
MS	31.8	37.6	27.5	24.1	20.7
SS	32.8	35.2	28.8	22.4	28.0
% Reduction	-	-	-	11	-

NS - Non stress

MS - Moderate stress

SS - Severe stress

*Significant at 0.05.

TABLE VI

RELATIVE CHANGES IN FIVE WINTER WHEAT CULTIVARS FOR SOME PHYSIOLOGIC CHARACTERS UNDER THREE MOISTURE LEVELS

Characters	Cultivars				
Stress levels	Blue Jacket	Kanking	TAM 101	Vona	Sturdy
Stomatal Resistance (Rs) Sec cm^{-1}					
NS	59.7 b*	54.7 b	46.1 a	46.7 a	43.1 b
MS	53.9 b	61.4 ab	53.6 a	51.8 a	33.1 b
SS	87.1 a	80.6 a	59.1 a	65.1 a	65.9 a
% Increase	46	47	28	40	53
Carbon Dioxide Exchange Rate (CER) mg CO_2 dm^{-2} hr^{-1}					
NS	5.20 a	4.31 a	3.60 a	3.01 a	3.56 a
MS	4.26 a	3.82 a	3.13 a	3.31 a	3.37 a
SS	4.37 a	2.98 a	3.60 a	2.43 a	2.00 b
% Reduction	13	31	0	19	44

NS - Non stress

MS - Moderate stress

SS - Severe stress

*Significant at 0.05.

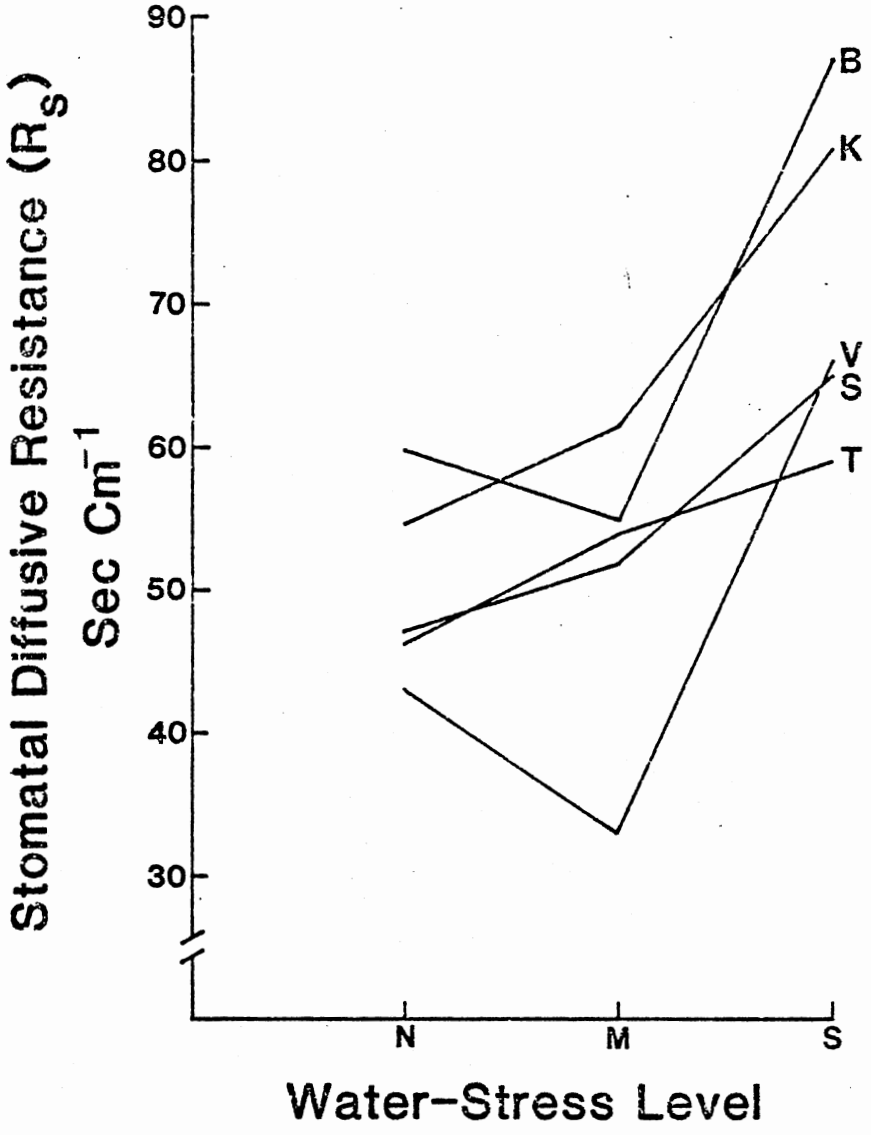

Figure 2. Stomatal Diffusive Resistance of 5 Winter Wheat Cultivars Under 3 Levels of Water-Stress

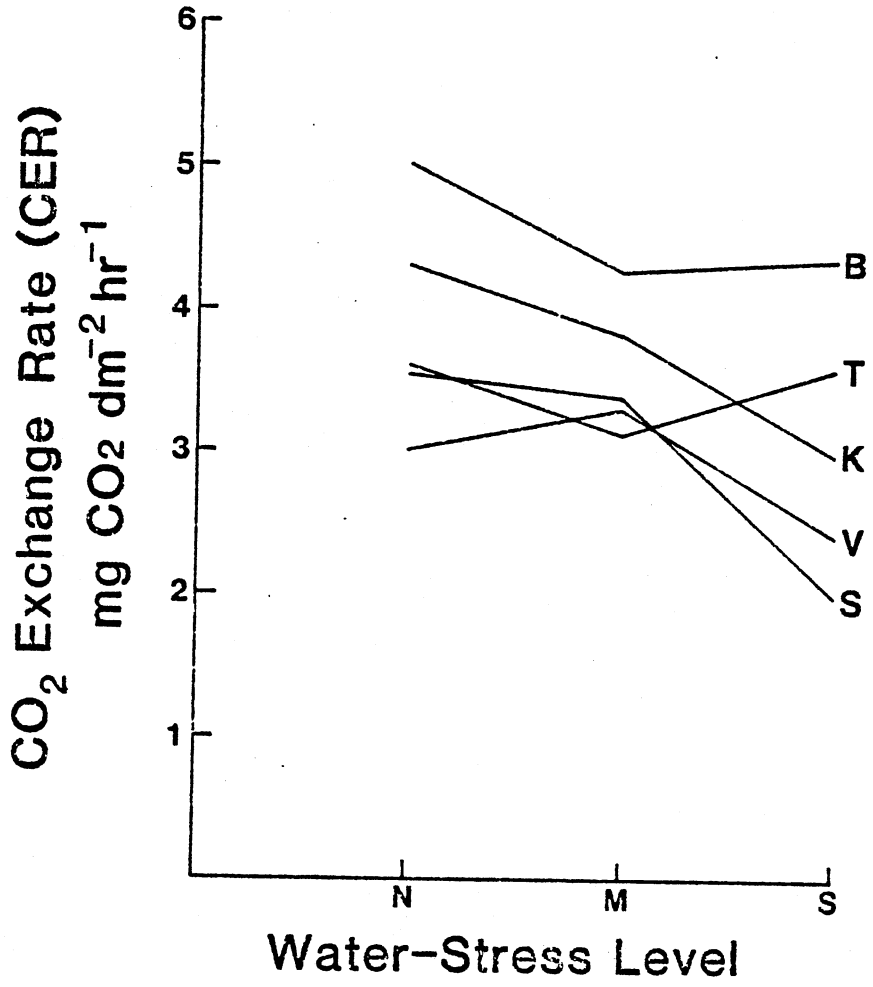

Figure 3. Carbon Dioxide Exchange Rate of 5 Winter Wheat Cultivars Under 3 Levels of Water-Stress

better adaptation to dry conditions for Blue Jacket than Sturdy.

The simple correlation coefficients for ten characters of five winter wheat cultivars under three moisture levels are presented in Table VII. Total dry matter is highly correlated with CER. Grain yield and CER association was positive but not significant. The correlation between total dry matter production and grain yield was highly significant (r=0.65). The relation of grain yield and HI was significant (r=0.62). The results suggest that by improving the CER of new genotypes, the accumulation of assimilate will increase. By improving the HI, a greater portion of assimilate could be incorporated into production of economic yield.

The stability of HI under three moisture levels shows that it can be used as a selection criteria as well as high CER for developing wheat cultivars to perform well under drought conditions.

Based on multiple regression analyses using a general linear models procedure, the relative importance of different plant characters on grain yield and total dry matter production are reported in Tables VIII and IX, respectively. Presence of CER in an eight variable model was significant for prediction of total dry matter production. This agreed with both sequential and partial sums of squares. In prediction of grain yield in an eight variable model, the intercept, kernel weight, and HI was significant.

TABLE VII

SIMPLE CORRELATION COEFFICIENTS FOR TEN CHARACTERS OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Plant Character	Plant Character 2	3	4	5	6	7	8	9	10
1. Total Dry Matter	.65**	.34*	.24	.03	.40**	-.09	.49**	-.18	-.17
2. Grain		.12	.12	.00	.23	.08	.14	.62**	.15
3. Kernel Weight			-.42**	.13	.34*	.47**	.29	-.18	-.11
4. Productive Tiller				-.25	.06	-.48**	.12	-.12	-.12
5. Kernel/Spike					.20	-.00	-.04	.00	-.09
6. Height						.14	.31*	-.15	-.24
7. Stomatal Resistance							-.10	.21	.01
8. CER								-.26	-.03
9. Harvest Index									.42**
10. Leaf Area									

Significant values for the correlation coefficients are 0.28 and 0.37 at the 5% and 1% level of probability, respectively (43 degrees of freedom).

TABLE VIII

RELATIVE IMPORTANCE OF DIFFERENT PLANT CHARACTERS (PARAMETERS) ON GRAIN YIELD OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Total Grain Yield Parameter	Regression Sum of Squares		Coefficient Estimate
	Sequential	Partial	
Intercept			-5.80* ±2.37
Rs	0.89	1.34	-0.01 ±0.01
CER	3.05	2.72	0.27 ±0.19
Kernel Weight	0.23	7.34	1.04* ±0.44
Tiller	4.54	4.59	0.11* ±0.06
Kernel/Spike	0.35	0.02	-.002 ±0.02
Height	2.08	2.81	0.02 ±0.01
Harvest Index	70.02**	63.63**	26.88**±3.93
Leaf Area	0.78	0.78	-0.07 ±0.09

*Significant at 0.05.
**Significant at 0.01.

TABLE IX

RELATIVE IMPORTANCE OF DIFFERENT PLANT CHARACTERS (PARAMETERS) ON TOTAL DRY MATTER OF FIVE WINTER WHEAT CULTIVARS UNDER THREE MOISTURE LEVELS

Total Dry Matter Parameter	Regression Sum of Squares		Coefficient Estimate
	Sequential	Partial	
Intercept			3.96 ±7.89
Rs	7.1	10.5	-0.03 ±0.04
CER	222.1**	62.4*	1.28*±0.63
Kernel Weight	66.4*	76.2*	3.36*±1.49
Productive Tiller	72.8*	49.1	0.36 ±0.20
Kernel/Spike	6.1	0.8	0.02 ±0.07
Height	20.6	17.7	0.06 ±0.01
Harvest Index	3.1	6.2	8.37±13.07
Leaf Area	4.5	4.5	-0.17 ±0.31

*Significant at 0.05.
**Significant at 0.01.

Summary

The results indicate:

1. Improved WUE through a mechanism expressed by drought tolerant wheat cultivars.
2. This represents a very important mechanism in that a cultivar that controls excessive transpiration with higher stomatal diffusive resistance can have higher CER at the same time. Some cultivars showed a higher CO_2 exchange rate and higher stomatal diffusive resistance which could control excessive transpiration.
3. A significant positive correlation between CER and total dry matter production was obtained.
4. In prediction of total dry matter, the presence of CER in a multiple regression model was significant.
5. The results suggest the possibility of improving winter wheat through incorporation of higher CER and proper stomatal behavior under drought conditions.

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CHAPTER V

HERITABILITY AND INTERRELATIONSHIP OF SOME OF THE PHYSIOLOGICAL TRAITS IN A CROSS OF WINTER WHEAT (*TRITICUM AESTIVUM* L. EM THELL)

Introduction

Considerable emphasis is given to yield improvement of winter wheat (*Triticum aestivum* L. em Thell) under good growing conditions. Much less progress has been made in improvement of yield under limited soil moisture.

Drought susceptibility of wheat is a problem in most arid and semi-arid regions of the world where wheat is grown under less than optimum rainfall conditions. The physiological understanding of drought resistance is not fully elucidated. The quantitative measurement and relationship of drought resistant plant characters to yield are not fully understood.

An understanding of the constraint of water on yield and the adaptation of plants to water deficits, challenges both the breeder to produce a cultivar that will give a greater yield under water-limited conditions, and the agronomist to ensure that the most efficient use is made of the available water. Selecting for high and stable yield under conditions of water stress likely to be encountered by the crop is

expensive and time consuming (Turner and Begg, 1981). The great variability from year to year in available soil moisture (Smith and Harris, 1981) means that selection has to be done over many seasons and selection indices and pressures vary from season to season. Under subpotential yield levels, heritabilities of yield and yield components are relatively low, and selection for yield is less efficient (Roy and Murty, 1970).

Wallace et al. (1972) concluded that almost all biochemical and physiological processes in plants are relevant to yield. Thus, incorporation of genes that affect photosynthesis may change a single enzyme or biochemical system that influences yield. They cite heritability data for many physiological components of yield such as relative growth rate, net assimilation rate, leaf area, leaf angle, net CO_2 exchange rate, stomatal number. stomata resistance and photorespiration. Generally broad-sense heritabilities were close to 60% which demonstrates genetic control of these components. Narrow-sense heritabilities were generally low but they increased with advancing generations. Thus, there is ample opportunity to improve any of these characteristics by selection.

Wallace et al. (1972) stated that selecting parents for crosses on the basis of potential physiological complementation will give, on the average more high yielding progenies than crosses between parents for which little is known.

Choice of the most efficient breeding procedures depends to a large extent on knowledge of the genetic systems controlling the characters under selection. Estimate of genetic variance and heritability provide

useful guidelines in directing in plant breeding programs.

This research was designed to study the association of some physiological traits with drought resistance in a winter wheat cross and estimate their heritabilities. Based on the objectives a cross of diverse parents (drought resistant and non-resistant) and their progenies were grown under field conditions.

Materials and Methods

The seed of P_1, P_2, F_1, F_2, BC_1 and BC_2 populations were derived from two hard winter wheat cultivars, 'Blue Jacket' and 'Sturdy'. Blue Jacket C. I. 12502 was selected from a field of super hard Blackhull by Earl G. Clark, a former wheat breeder at Sedgwick, Kansas. Sturdy was developed by the Texas Agricultural Experimental Station and is semi-dwarf with strong straw. These two cultivars were chosen as parents of their diversity for the physiolgic traits related to drought resistance previously studied.

To insure uniform spacing and stands, the seeds of all entries were germinated in glass cylinders (bubble germinator), a method for germinating small quantities of seed in the laboratory described by Darby and Saller (1976). The germinated seeds were planted in paper bands in flats containing a mixture of soil and vermiculite. The seedlings were grown in the growth chamber for a week and then placed outside for hardening before transplanting. The seedlings were transplanted on October 22, 1981 in a randomized complete block design at the Stillwater Agronomy Research Station. The experiment consisted of three replications, each composed of 11 experimental rows as

Rows were spaced 30 cm aparted and contained seven plants spaced 30 cm apart with all measurements taken on an individual plant basis. There were two border rows around each replication. The following data were collected on seven plants in a row, the data of six plants were used in analyses in order to have equal sample size per row.

Total Dry Matter - Total weight in grams of the total above ground dry matter of each plant.

Grain Yield - Total weight in grams of the seed from each plant.

Harvest Index (HI) - Calculated as ratio of grain yield over total dry matter.

Plant Height - Measured on each single plant from the base of the tillers to the tip of the terminal spikelet (exluding awns).

Peduncle Length - Measured as the distance from auricle to the base of spike.

Flag Leaf Area - Measured using a portable LI-COR L13000 Leaf Area Meter (LI-COR Inc., Lincoln, Nebraska).

Flag Leaf Width - Measured at the maximum width of the leaf.

Stomatal Diffusive Resistance (Rs) - Measured by using Steady State Prometer (LI-1600((LI-COR, Inc., Lincoln, Nebraska).

Photosynthesis measurements were taken from a single leaf placed in a plexiglass chamber 6.4 cm long x 2.9 cm in diameter as discussed in Materials and Methods (Osmanzai, 1982).

Estimates of (a) environmental, (b) additive, and (c) dominance variances for each character were calculated for each entry averaged over replications. The following formulas were used to derive these variances:

TABLE I

ENTRIES AND ROW NUMBER

Population	No. of rows per replication
P_1 (Blue Jacket)	1
P_2 (Sturdy)	1
F_1 (P_1 x P_2)	1
F_2 (F_1 selfed)	4
BC_1 (Backcross of F_1 to P_1)	2
BC_2 (Backcross of F_1 to P_2)	2

(a) $\sigma^2E(x) = 1/3[\ Var(x)P_1 + Var(x)P_2 + Var(x)F_1]$

(b) $\sigma^2A(x) = 2\ Var(x)F_2 - [\ Var(x)BC_1 + Var(x)\ BC_2]$

(c) $\sigma^2D(x) = Var(x)F_2 - [\sigma^2A + \sigma^2E]$

where $\sigma^2E(x)$, $\sigma^2A(x)$ and $\sigma^2D(x)$ represent estimates of environmental, additive and dominance variance for character x, respectively. In this context, σ^2A and σ^2D are equivalent to 1/2 D and 1/4 H, respectively, as described by Mather and Jinks (1971). $Var(x)P_1$, $Var(x)P_2$, $Var(x)F_1$, $Var(x)BC_1$ and $Var(x)F_2$ represent the variance of character (x) of the P_1, P_2, F_1, BC_1, BC_2 and F_2 generations respectively. Each term in the above formulas was based on estimates of within-row variance components.

Heritabilities estimates for each character studied were calculated using the variance component estimates previously described and are reported for each character as the mean of the estimate calculated for each of 2 replications (CER and Rs) and 3 replications (other characters). Broad sense heritabilities, h^2bs were estimated as a ratio of additive and dominance variance to the total variance as:

$$h^2bs = \frac{\sigma^2A(x) + \sigma^2D(x)}{\sigma^2A(x) + \sigma^2D(x) + \sigma^2E^2(x)}$$

The narrow-sense estimates, h^2ns, were estimated as a ratio of the additive variance to the total variance as:

$$h^2ns = \frac{\sigma^2A(x)}{\sigma^2A(x) + \sigma^2D(x) + \sigma^2E^2(x)}$$

Interrelationships among the plant characters were studied by computing phenotypic correlation coefficients among all possible pairs of variables. Phenotypic correlation coefficients were calculated using the variance and covariances of the F_2. The phenotypic (rp) correlations were calculated on a plant basis as:

$$rp = \frac{Cov(x,y)F_2}{[Var(x)F_2 \cdot Var(y)F_2]^{1/2}}$$

where $Cov(x,y)F_2$ represent the covariances between character x and y in F_2 and $Var(x)F_2$ and $Var(y)F_2$ represent the variance of x and y in the F_2.

Results and Discussion

Parental means, standard errors and coefficients of variation of the characters studied are reported in Table II. Blue Jacket had higher biological yields, was taller, had longer peduncle lengths, higher CER, and lower HI than Sturdy. Sturdy had a slightly higher Rs. Due to wet conditions encountered during heading when measurements were to be taken, only a few measurements were taken. Also, water stress conditions did not appear. Therefore, the association of characters studied and their h^2 are considered only for non-stress conditions. Means, variances, and coefficients of variation of BC_1, BC_2, F_1, and F_2 are presented in Tables III and IV, respectively.

Estimates of additive, dominance and environmental variances as well as h^2bs and h^2ns are presented in Table V. Environmental variation was much more important than additive or dominance gene action for all the characters studied except HI and Rs. Additive gene action was higher than environmental variance for HI. It was positive for grain yield also. A dash is shown for negative estimates. Walton (1969) using a diallel cross of seven spring wheats showed that flag leaf area, peduncle length, head length and yield were all controlled by minor genes. Additive gene action and general combining ability were shown to

TABLE II

PARENTAL MEANS, STANDARD ERRORS AND COEFFICIENTS OF VARIATION FOR THE CHARACTERS STUDIED

Character	Blue Jacket (P_1)		Sturdy (P_2)	
	Mean SE	CV, %	Mean SE	CV, %
Total Dry Matter, g	27.93±3.1	39	19.40±2.22	38
Grain Yield, g	5.98±0.75	43	5.71±0.84	49
Harvest Index	21.41±0.92	15	29.42±2.37	27
Height, cm	88.50±2.04	9	58.36±2.14	12
Peduncle Length, cm	17.53±0.87	17	10.29±0.33	11
Flag Leaf Area, cm^2	15.81±1.43	31	15.30±1.17	25
Flag Leaf Width, cm	1.28±0.038	7	1.31±0.05	13
Photosynthesis (CER), mg dm^{-2} hr^{-1}	7.42±0.85	40	6.10±0.68	37
Stomatal Resistance, sec cm^{-1}	1.71±0.20	42	2.29±0.19	27

TABLE III

BACKCROSSES MEANS, VARIANCES AND COEFFICIENTS OF VARIATION FOR THE CHARACTERS STUDIED

	BC_1			BC_2		
Character	Mean	Variance	CV, %	Mean	Variance	CV, %
Total Dry Matter	25.24	105.93	41	24.20	62.09	33
Grain Yield	7.03	7.78	40	7.54	6.19	33
Harvest Index	27.80	18.71	16	31.50	43.94	21
Height	83.58	54.25	9	68.33	52.55	11
Peduncle Length	19.97	11.95	18	15.58	6.48	16
Flag Leaf Area	13.79	21.22	33	14.82	27.20	35
Flag Leaf Width	1.22	0.03	15	1.30	0.04	16
Photosynthesis (CER)	5.42	8.41	53	5.93	5.40	39
Stomatal Resistance	2.21	1.22	50	2.54	3.90	78

TABLE IV

F_1 AND F_2 MEANS, VARIANCE AND COEFFICIENTS OF VARIATION FOR THE CHARACTERS STUDIED

	F_1			F_2		
Character	Mean	Variance	CV, %	Mean	Variance	CV, %
Total Dry Matter	22.11	23.20	22	24.89	65.24	32
Grain Yield	6.96	11.09	48	6.45	8.48	45
Harvest Index	30.75	77.54	29	26.30	61.16	30
Height	72.08	112.68	15	75.31	44.17	9
Peduncle Length	15.60	26.35	33	15.24	8.81	19
Flag Leaf Area	14.76	14.53	26	14.98	22.25	31
Flag Leaf Width	1.25	0.05	18	1.24	0.03	14
Photosynthesis (CER)	6.86	5.87	35	6.30	5.61	38
Stomatal Resistance	2.26	1.16	48	2.35	1.52	52

TABLE V

ESTIMATES OF ADDITIVE, DOMINANCE, AND ENVIRONMENTAL VARIANCES AND BROAD AND NARROW-SENSE HERITABILITIES FOR THE CHARACTERS STUDIED

Character	Additive Variance	Dominance Variance	Environmental Variance	h^2 Broad-Sense	h^2 Narrow-Sense
Total Dry Matter	-	38.09	64.69	-	-
Grain Yield	2.99	-	8.49	-	-
Harvest Index	59.67	-	49.78	0.19	0.98
Height	-	-	75.89	-	-
Peduncle Length	-	-	-	-	-
Flag Leaf Area	-	8.16	18.01	0.37	-
Flag Leaf Width	-	0.01	0.03	0.33	-
Photosynthesis (CER)	-	1.66	6.54	0.30	-
Stomatal Resistance	-	2.92	0.68	0.55	-

- Equal to a negative number for which best estimate was zero.

be important genetic factors for the characters mentioned.

Broad sense heritability estimates were low for HI (0.19), flag leaf area (0.37), flag leaf width (0.33), and CER (0.30). The estimated h^2bs for Fs was moderate (0.55). The narrow sense heritability estimate was high for HI (0.98).

These results indicate that HI and Rs would be characters responsive to selection. There is not much information available on h^2 of Rs. Some studies have been done on stomatal number and size. If the selection is for stomatal frequency alone, parallel changes in stomatal size may compensate for any reduction in frequency, and this may eliminate any effect on lead conductance (Jones, 1977).

Stomatal characters such as size, and frequency per unit leaf area have been shown to have high heritabilities in a range of species (Tan and Dunn, 1976). Henzell et al. (1976) and Rork and Quisenberry (1977) provided some evidence that low conductance, or at least high sensitivity to stress, is dominant. Since anatomical characters alone are not reliable indicators of relative transpiration rate, it is still necessary to screen for conductance directly. It is suggested that improvement in crop water use efficiency could be achieved by selection for higher CER and proper stomatal aperature, (Osmanzai and Croy, 1982; Osmanzai, 1982).

Phenotypic correlation coefficients between all possible pairs of characters are presented in Table VI. Total dry matter production was significantly correlated to grain yield and flag leaf area (0.69 and 0.41), respectively. Grain yield was highly correlated to HI (0.65) and negatively to stomatal resistance (-0.38). Harvest index was positively

TABLE VI

PHENOTYPIC CORRELATIONS BETWEEN ALL POSSIBLE PAIRS OF CHARACTERS STUDIED

Character	2	3	4	5	6	7	8	9
1. Total Dry Matter	.69**	-.06	.50**	.12	.41*	.18	.03	-.24
2. Grain Yield		.65**	.24	.08	.32	.14	.32	-.38*
3. Harvest Index			-.21	.01	-.09	-.07	.35*	-.25
4. Height				.36*	.29	.21	.22	-.17
5. Peduncle Length					.18	-.24	-.06	-.04
6. Flag Leaf Area						.43**	.12	-.33
7. Flag Leaf Width							.20	-.28
8. Photosynthesis (CER)								-.47**
9. Stomatal Resistance								

Correlation coefficient with n-2=46 must exceed 0.35 and 0.43 to be significant at the 0.05 and 0.01 probability level respectively.

correlated to CER (0.35). Association between plant height and peduncle length was positive (0.36). As expected, a highly positive, significant r (0.43) between leaf area and leaf width was obtained. The association between CER and Rs was negative (-0.47).

The negative relationship of grain yield with Rs in this study could be due to inhibition of photosynthesis by reduction of CER as indicated by the negative association of CER and Rs. Since soil moisture was not a limiting factor due to adequate rainfall the regulation of water loss by the stomata probably did not affect yield.

Summary

Stomatal diffusive resistance (Rs) has a medium (0.55) h^2bs, and CER (0.3) h^2bs. A negative phenotypic correlation (r=-0.47) between CER and Rs was obtained. The results suggest that in improving stomatal aperature, CER must be considered and parents should be selected based on their complimentation for the above traits.

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VITA

Mahmood Osmanzai

Candidate for the Degree of

Doctor of Philosophy

Thesis: SOME PHYSIOLOGICAL ASPECTS OF DROUGHT RESISTANCE IN WINTER WHEAT (TRITICUM AESTIVUM L. EM THELL)

Major Crop: Crop Science

Biographical:

Personal Data: Born in Kabul, Afghanistan, August 1, 1945, the son of Mr. and Mrs. Mohammad Osman.

Education: Graduated from Kabul Vocational Agricultural School in Kabul, Afghanistan, in December, 1964; received Bachelor of Science degree in Agriculture from Faculty of Agriculture, Kabul University, Kabul, Afghanistan, in February 1969; completed the requirements for a Master of Science degree at Oklahoma State University in December, 1974, and completed the requirements for the Doctor of Philosophy degree in Crop Science at Oklahoma State University in December, 1982.

Professional Experience: Worked at the Department of Research and Soil Science, Ministry of Agriculture and Irrigation, Kabul, Afghanistan, from 1970 to 1972; and from 1975 to 1978 as Research Agronomist, and from 1978 to 1979 as Research Cereal Improvement Specialist. Graduate Research Assistant, Department of Agronomy, Oklahoma State University, Stillwater, Oklahoma, 1980 to 1982.

Military Service: Afghan Army, March, 1969, to April, 1970, 3rd Lieut.

Professional Organization: American Society of Agronomy and Crop Science Society of America.